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Letters to the Editor

Low air humidity increases aggressiveness of ixodid ticks (Acari: Ixodidae) under high ambient temperatures (a preliminary hypothesis)



It has been established that the brown dog tick *Rhipicephalus sanguineus* sensu lato rarely attacks humans (Walker et al., 2000; Parola and Raoult, 2001). Sometimes, however, notable exceptions have been observed, especially in the Mediterranean countries (Gilot et al., 1990; Wilamowski et al., 1999; Otranto et al., 2014). Recently it was experimentally demonstrated that under high temperature conditions all parasitic stages of *R. sanguineus* s.l. ticks increase their aggressiveness towards hosts and readily attach to humans (Parola et al., 2008; Socolovschi et al., 2009). Epidemiological and clinical data summarized by Parola et al. (2008) support the conclusion that warmer weather increases the tendency of this species to attack humans and infect them with rickettsiae. However, the biological mechanisms underlying the observed relationship between temperature and aggressiveness in *R. sanguineus* s.l. remain unknown.

For more than a century, temperature has been recognized as the most important environmental factor influencing all aspects of poikilothermic animals' life (Mednikov, 1977 [2005]). Due to the gradual warming of the Earth's climate taking place at the present time, the temperature factor has become especially important (Gray et al., 2009; Dantas-Torres, 2015). Although air temperature has been considered to be the leading abiotic factor determining all aspects of the lives of terrestrial arthropods, such factors as air humidity, soil moisture and precipitation are also of high importance for ticks (Daniel and Dusbábek, 1994).

We propose that (i) the positive correlation between ambient temperature and tick aggressiveness is not limited to *R. sanguineus* s.l. but is typical of other tick species, and (ii) the elevated aggressiveness of ticks at higher temperatures is mostly driven by reduced air humidity rather than being a direct effect of temperature. Our hypothesis is based on our previously unpublished data and limited published observations of the behavioral patterns on adult *Ixodes* ticks under different environmental conditions.

In May–June of 1966–1969, we collected hundreds of adult *Ixodes persulcatus* ticks (the taiga tick) in mid-highland mixed forests of the Western Sayan Mountains for utilizing these ticks in toxicological tests. The forests were characterized by the high tick abundance (Naumov, 1999). Four experienced persons in protective clothes collected ticks by flagging grass vegetation. The number of ticks collected by the flag and removed from collectors' clothes (the lower and upper parts separately) as well as the air temperature and relative air humidity (RH) before and after collecting were recorded. Our analysis is based on data sets containing at least 400 ticks per sample, collected over 2–2.5 h, which were obtained during the period of highest activity of the adult ticks (the last 2 weeks of May and the first 2 weeks of June). At that time, the height of grass canopy reached up 50 cm. We identified two pairs of samples with different values of air temperature (22–25 °C vs. 27–30 °C) but similar values of RH conditions (94–68%) and one pair of samples with the same values of air temperature (26–30 °C) but sharply differing

values of RH (100–76% vs. 68–50%). For each pair, we compared the percentage of ticks on flags and on collectors' clothes and the mean numbers of ticks per collector per hour of collection. Since the numbers of tick collected by individual personnel at the same area during the same collection period follow a normal distribution (according to our data accumulated over many years), we applied the Student's *t*-test in comparing the data sets, wherein the difference was deemed to be significant if $P < 0.05$.

When ticks were collected at lower and higher temperatures but at the same RH, the proportion of ticks removed from collectors as compared with that on flags increased with higher ambient temperatures (20.2% vs. 10.4%). The difference between the samples was highly significant ($P < 0.001$) both in the mean numbers of ticks per person as well as in the numbers of ticks removed from the lower and upper parts of the clothes. We suggest that the ratios of the numbers of ticks collected by flags to those removed from collectors' clothes at different temperatures indicate that the aggressiveness of adult *I. persulcatus* increases at higher ambient temperature, similar to observations on *R. sanguineus* s.l. (Parola et al., 2008). Okulova (1986, pp. 107, 112) also pointed out that the number of adult *I. persulcatus* attacking humans was 2–3 times higher when ambient temperature increased from 20–24 °C to 26–27 °C. The above data support the first element of our hypothesis that the relationship between ambient temperature and tick aggressiveness is typical of a broader range of exophilic tick species.

When evaluating the effect of ambient temperature on tick activity, it is important to keep in mind that air temperature negatively correlates with air humidity. The importance of air humidity for tick vitality has been noted by many researchers under field observations (e.g. Lees, 1946; Kheisin, 1953; Knülle, 1966) as well as in laboratory experiments (Perret et al., 2003; Crooks and Randolph, 2006). In our work when ticks were collected at the same temperatures but at contrasting RH levels, the proportion of ticks removed from collectors as compared with that on flags increased with lower RH (33.4% vs. 20.6%), 56.3% of which were removed from the upper part of collector's clothes. The difference between the samples was highly significant ($P < 0.001$) in the mean numbers of ticks per person as well as in the numbers of ticks removed from the upper part of the clothes. Under conditions of lower RH, two instances of tick attachment to collectors were observed, whereas there were no such cases under other conditions of collecting during all years of our work in the area.

Since elevated temperatures are usually associated with lower RH, which, in turn, increases water loss by ticks, such conditions are expected to favor tick behavior aimed at compensating dehydration. Typically, when air humidity is low, ticks move down to the litter level to restore their water content (moisture-seeking behavior). We speculate that when ticks sense the proximity of a host, they activate an alternative behavioral approach to restoring hydration by expediting their attachment to the host. According to many authors (reviewed by

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Kahl, 2018), the water content of the blood ingested by ticks is about 80% or more. In fact, hematophagy is considered as one of the ways for hydration in many groups of blood-sucking arthropods, including ticks (Benoit and Denlinger, 2010).

Our hypothesis about the primary importance of reduced air humidity in the elevated aggressiveness of ticks at higher temperatures is in line with the conclusion made by Okulova (1986, p. 109) that “air dryness noticeably enhances the impact of the temperature factor” on *I. persulcatus* activity. A similar conclusion was made by Herrmann and Gern (2010) for *I. ricinus*. The hypothesis is also in accordance with observations made in mosquitoes, where dryness increased their activity and a combination of low RH and high ambient temperature increased the rate of water loss and stimulated their blood-sucking activity (Hagan et al., 2018). Although an interaction of multiple factors must influence the behavior of ticks when off the host, air humidity seems to be dominant. Precisely controlled laboratory experiments on ticks of different species and stages are required to test the validity of this hypothesis.

The proposed hypothesis readily explains the observed increased aggressiveness of *R. sanguineus* s.l. towards humans in urban environment. Although this xerophilic species has special adaptations for water conservation (Yoder et al., 2006), adequate humidity is a very important factor for its successful existence (Gray et al., 2009), while its opportunities for water replenishment in urban habitats are likely to be limited. Since the development of urban environment is followed by creation of so-called urban heat islands and urban dry islands (Hage, 1975; Cuadrat et al., 2015; Yang et al., 2017), even ticks with low affinity for humans, finding themselves under conditions of high temperature and low humidity have little choice but to aggressively attack any suitable host to avoid desiccation. Taking into account the fact that ticks have become an ubiquitous component of the urban environment (Uspensky, 2017), and that among the tick species inhabiting cities and towns there are many forest species (such as *I. ricinus* and *I. persulcatus*) that are very sensitive to reduced air humidity (Shashina and Ioffe, 1980; Uspensky, 2002), it would be reasonable to anticipate an increased risk of tick-borne diseases in urban areas in the near future.

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